Primary production in the Labrador Sea and adjacent waters: Atlantic Zone Off-Shelf Monitoring Program 1991-2011

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ABSTRACT

Harrison, W.G. and W.K.W. Li 2015. Primary production in the Labrador Sea and adjacent waters: Atlantic Zone Off Shelf Monitoring Program 1991-2011. Can. Tech. Rep. Hydrogr. Ocean. Sci. 307: viii + 40 p.

Results from 20 years (21 missions) of environmental and photophysiological observations of natural phytoplankton populations in the Labrador Sea are reported. Variability in environmental (temperature, nutrients) and biological (phytoplankton biomass, photosynthetic characteristics) were linked to sampling depth, season and geographical location. Time of year of sampling made the greatest contribution to variability of most properties although geography differences were also important. Inter-annual variability was significant but longer term trends were weak or absent. Synoptic satellite ocean colour data have helped to fill in the gaps, due to the limited field sampling, in order to provide a more complete picture of regional productivity. The annual phytoplankton growth cycle in the Labrador Sea is marked by early spring blooms on the Labrador and Greenland shelves, a summer bloom in the central basin and a brief, geographically confined, fall bloom off the Labrador Shelf. Measured and modeled total and new primary productivity in the Labrador Sea is typical of sub-polar regions. To date, there is little evidence of long term changes in productivity in the Labrador Sea despite indications of some nutrient, phytoplankton community structure and photophysiological changes over the past 20 years. Field and satellite data collected in the Northwest Atlantic over the past 2-3 decades, as described here, underpin new model-based estimates of primary productivity that are providing unprecedented spatial and temporal detail of this fundamental ecological process.

RÉSUMÉ

Harrison, W.G. et W.K.W. Li, 2015. Production primaire dans la mer du Labrador et les eaux avoisinantes : Programme de monitorage de la zone Atlantique du talus, 1991-2011. Rapp. tech. can. hydrogr. sci. océan. 307: viii + 40 p.

Les résultats de 20 ans (21 missions) d'observations environnementales et photophysiologiques des populations naturelles de phytoplancton dans la mer du Labrador sont indiqués. Les variabilités des conditions environnementales (température, nutriments) et biologiques (biomasse du phytoplancton, caractéristiques photosynthétiques) ont été liées à la profondeur d'échantillonnage, la saison et l'emplacement géographique. Les périodes de l'année auxquelles les échantillonnages ont été effectués ont constitué la plus grande contribution à la variabilité de la plupart des propriétés, bien que des différences géographiques aient été également importantes. La variabilité interannuelle a été importante, mais les tendances à long terme ont été faibles ou inexistantes. Les données satellitaires synoptiques sur la couleur des océans ont aidé à combler les lacunes découlant du nombre limité d'échantillonnages en mer, afin de fournir un portrait plus complet de la productivité régionale. Le cycle annuel de croissance du phytoplancton dans la mer du Labrador est marqué par des proliférations printanières précoces sur les plateaux du Labrador et du Groenland, une prolifération estivale dans le bassin central et une brève prolifération automnale, géographiquement restreinte, au large du plateau du Labrador. La récente productivité primaire totale mesurée et modélisée dans la mer du Labrador est typique des régions subpolaires. Jusqu'à maintenant, il y a peu de preuves de changements à long terme dans la productivité dans la mer du Labrador malgré les indications de certains changements concernant les nutriments et la structure des communautés phytoplanctoniques et de certains changements photophysiologiques survenus au cours des 20 dernières années. Les données recueillies par échantillonnages en mer et par satellite dans le nord-ouest de l'Atlantique durant les deux ou trois dernières décennies, tel qu'il est décrit dans le présent document, servent de fondement à de nouvelles estimations de la productivité primaire fondées sur un modèle qui fournissent des détails spatiaux et temporels sans précédent sur ce processus écologique fondamental.

1. INTRODUCTION

Primary productivity has been long recognized as a key process that regulates energy flow and structure of marine ecosystems. However, in the last few decades, scientific research on ocean biogeochemistry has also highlighted the crucial role that primary productivity plays in the global carbon cycle and contributes to important oceanic feedbacks to the climate system under climate change. Sub-polar regions, such as the Labrador Sea, are biologically highly productive and have been identified as active sites of carbon sequestration, mediated by both physical and biochemical processes. Understanding and quantifying these processes has been an important over-arching goal of the long-standing Atlantic Zone Off-shelf Monitoring Program (Greenan et al, 2010).

Although primary productivity has not been designated a core variable in the suite of biological measurements made by the Atlantic Zone Off-shelf Monitoring Program, routine measurements of photosynthesis-irradiance (P-I) parameters since 1991, periodic (1999-2004) measures of column primary productivity and synoptic satellite-based observations of surface chlorophyll (1998-2012) provide sufficient observations to evaluate some aspects of the spatial and temporal variability of phytoplankton growth dynamics in the region.

Here we provide a description of the spatial distribution and temporal variability of photosynthetic properties and selected environmental conditions in the Labrador Sea area. This present report on primary productivity, taken together with companion reports on the state of phytoplankton and bacterioplankton in the Labrador Sea (Li and Harrison 2014) and on ammonium distribution in the Labrador Sea and adjacent waters (Harrison 2013), collectively comprise an integrated set of measurements for the primary[1] biological component of the Atlantic Zone Off-Shelf Monitoring Program.

This account is not a comprehensive analysis of the processes that govern regional productivity but a summary of observations over the past two decades that should inform discussion on leading hypotheses (Harrison et al. 2013), helping to explain some of the unique features of phytoplankton growth in the Labrador Sea. Thus, the purpose of this report is to provide information useful for a more thorough analysis of primary productivity in the region and its biogeochemical significance.

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[1] i.e. excluding zooplankton

2. METHODS

2.1 SAMPLING

Primary sampling was done along the "L3 Line", also referred to as the "AR7/W" WOCE repeat hydrographic section (Yashayaev 2007). Discrete samples were collected at 30-31 nominal stations from the Labrador to Greenland coasts (Figure 1). For each of the 28 stations designated by the core program, the geo-location, ocean bottom depth, and section distance are tabulated in Li and Harrison (2014). We group the stations into 3 nominal regions: the Labrador Shelf and Slope (LSS) for stations 1-10; the Central Labrador Basin (CLB) for stations 11-23; and the Greenland Shelf and Slope (GSS) for stations 24-28. According to this nominal assignment, CLB extends over a region where ocean bottom depth exceeds 2900 m; LSS covers the region of shallower depths to the west, and GSS covers the region of shallower depths to the east.

Water samples were collected using a CTD-rosette system outfitted with 24 10L PVC sampling bottles. Water samples were collected from 11 depths (shallow stations <200 m) to 24 depths (deep stations to >3600 m depth) along the line. Additional stations along other lines or in transit to and from L3 were sampled in some years. Biological sampling along the L3 line began in 1991 and the line has been occupied at least once annually since 1994, 21 missions in 20 years, mostly in spring/early summer (Table 1, Figure 2). Annual occupation of stations in the Labrador Sea area ranged from 4-26 days (average = 11 d) and started as early as the second week in May to as late as the first week in December (Table 1).

2.2 ANALYTICAL

Nutrients (NO_3, PO_4, SiO_3) were measured on all missions using standard auto-analyzer methods (Technicon II). Ammonium (NH_4) was also measured on occasion but dealt with in another report (Harrison 2013). Chlorophyll *a* (CHL) was measured fluorometrically (Holm-Hansen et al. 1965). Vertical chlorophyll profiles parameters were based on a shifted Gaussian fit of the field data (Platt and Jassby 1976, Platt et al. 1988). Particulate organic carbon (POC) and nitrogen (PON) were determined by high-temperature combustion (Perkin-Elmer Elemental Analyzer). Vertical profiles of physical properties of the water column (e.g. temperature, salinity, irradiance) and fluorescence were measured continuously using an instrumented CTD-rosette system (Seabird SBE 25, LICOR, Chelsea Instruments).

Primary productivity of natural phytoplankton assemblages was measured in two ways: (i) ^{14}C tracer experiments using linear white light incubators from which photosynthesis-irradiance (P-I) parameters were derived (Platt et al. 1980) or (ii) ^{13}C

and ^{15}N tracer experiments using surface seawater cooled deck incubators under natural light from which "simulated" *in situ* (SIS) productivity profiles were derived (Moran et al. 2003). Samples for P-I experiments were collected at 2-3 depths: surface mixed layer (0-10 m), below the mixed layer and often at the subsurface chlorophyll maximum (CHLmax) layer (15-30 m) and, on occasion (~25% of the stations), below the CHLmax (40-60 m). Samples for SIS experiments were collected at 8 depths from surface to the 0.1 % light penetration depth.

Satellite sea surface temperature (SST) and ocean colour data were extracted and images produced from SeaWiFS and MODIS missions (http://www.bio.gc.ca/science/newtech-technouvelles/sensing-teledetection/index-eng.php). Spring bloom parameters (timing, amplitude, duration) were derived from a shifted Gaussian fit of the satellite data (Zhai et al. 2011). Satellite-based chlorophyll, SST and incident irradiance data were combined with chlorophyll profile and P-I parameters from field measurements to derive synoptic column-integrated primary productivity estimates (Platt el al. 2008).

3. RESULTS

Samples for productivity measurements (P-I) and environmental variables were collected at 266 stations (5-36 stations/mission) between 1991 and 2011 (Table 1). Fewer samples (66) were collected for SIS productivity measurements (7-18/mission) and only during the 1999-2004 missions. For the environmental variables, a comprehensive description of the entire spring/summer sample collection is given in the companion report (Li and Harrison 2014); however for present purposes, only the subset of these environmental variables sample-matched to the primary productivity measurements is considered. Satellite data and images were produced bi-weekly (SeaWiFS: 1998-2010; MODIS: 2003-2012). Basic statistics were generated from the satellite data for the L3 line and three sub-regions representing the Labrador Shelf/Slope, LSS, the Central Labrador Basin, CLB, and the Greenland Shelf/Slope, GSS (Figure 1).

3.1 PHOTOSYNTHESIS-IRRADIANCE (P-I) PARAMETERS AND ENVIRONMENTAL VARIABLES

Predictably, nutrient concentrations generally increased with depth of sampling but were highly variable within a depth horizon (Table 2). Particulates, on the other hand, were usually highest in the mid-depth range associated with the subsurface CHLmax

layer, although overall not significantly different from concentrations at the surface; concentrations dropped off significantly in the deeper waters, below the CHLmax. P-I parameters varied with depth as well with maximum photosynthetic rates (Pmax) decreasing with depth and photosynthetic efficiency (α) increasing with depth; the so-called photo-adaptation parameter (Ik) decreased with depth. Experimental incubation temperatures (adjusted to ambient conditions) also decreased with depth.

Regional differences in productivity and environmental variables were also noted. NO_3 concentrations were highest in the central Labrador Basin and SiO_3 and PO_4 concentrations were lowest on the Greenland Shelf (Table 3). Particulates, in contrast, were highest on the Greenland Shelf, followed by the Labrador Shelf, and lowest in the central Labrador Basin. Chlorophyll profiles parameters were consistent with particulates showing highest background chlorophyll levels (Bo) and column-integrated levels (h) on the Greenland Shelf. The depth of the subsurface chlorophyll maximum (Zmax) was similar among sub-regions but the width of the maximum (σ) was greatest in the central Labrador Basin. Despite the fact that incubation temperatures were highest in the central Labrador Basin, P-I parameters (α and Pmax) were highest on the Greenland Shelf but Ik was similar among the three sub-regions.

The largest contrast in environmental variables was seen in time of year of sampling. Highest NO_3 and PO_4 concentrations were observed in October-December, concentrations were somewhat reduced in May and decreased significantly over the next two months, June-July (Table 4). SiO_3 concentrations, in contrast, were higher in May than in fall/winter but decreased dramatically by July. Particulates were highest in May and progressively decreased to very low levels in December (Table 5). Chlorophyll profiles parameters (Bo and h) also progressively decreased from May-December, however, the depth of the CHLmax (Zmax) was shallowest in June and deepest in December; the width of the CHLmax layer (σ) was at a minimum in June and maximum in October (Table 6). Despite the seasonal differences in incubation (and *in situ*) temperatures (minimum in December, maximum in July), P-I parameters (α and Pmax) were generally comparable among seasons with the exception of October where levels were unusually low; Ik values were lower in October-December than in May-July (Table 7).

A more detailed picture of the spatial variability in productivity and environmental variables can be seen in the distribution of properties along the L3 line during the May-June missions when/where most of the sampling occurred (see Figure 2) and large spatial scale and seasonal effects were minimized. NO_3 concentrations were lowest on the Labrador Shelf, peaked in the central Labrador Basin and decreased to intermediate levels on the Greenland Shelf (Figure 3). PO_4 and SiO_3 concentrations were highest on the Labrador Shelf and decreased gradually from west to east. Nutrient ratios indicated

a surplus of PO_4 (relative to NO_3) across the entire line but especially so on the Labrador Shelf whereas a surplus of SiO_3 (relative to NO_3) was only seen on the Labrador Shelf and SiO_3 was at a deficit across the central Labrador Basin and up to the Greenland Shelf. Particulates were highest on the Labrador and Greenland Shelves and lowest in the central Labrador Basin; particulate C:N ratios were relatively stable across the L3 line and were generally above the "Redfield" ratio (Figure 4). Chlorophyll profile parameters showed some similarity in the distribution of background chlorophyll (Bo) and column-integrated (h) levels with particulate distributions, i.e. highest on the two shelves; there was a tendency for the depth of the CHLmax (Zmax) and the width of the layer (σ) to increase slightly west to east (Figure 5). P-I parameters (α and Pmax) tended to increase from the Labrador Shelf through the central Labrador Basin, paralleling incubation (and *in situ*) temperatures. However, on the Greenland Shelf, Pmax decreased abruptly along with temperatures while α remained at or above levels seen in the central basin; as a consequence of this divergence of Pmax and α, Ik also decreased abruptly in the east (Figure 6).

Using the same subset of data (i.e. May-June missions along the L3 line), inter-annual variability in productivity and environmental variables was evaluated. There were no strong temporal trends in nutrient concentrations or nutrient ratios although SiO_3 concentrations showed some decrease with time resulting in an increasing Si-deficit relative to NO_3; with a few exceptions, the L3 line could be characterized as PO_4-rich and SiO_3-deficient for the entire time-series (Figure 7). Similarly, no strong temporal trends were apparent in particulates (Figure 8). Chlorophyll profile parameters, however, appeared to increase somewhat over time, particularly column-integrated levels (h) and width (σ) of the subsurface CHLmax (Figure 9). With exception of the 1991 data, there appeared to be a modest increase in P-I parameters with time (Figure 10).

3.2 SATELLITE REMOTE-SENSING OF OCEAN COLOUR: PHYTOPLANKTON BIOMASS DISTRIBUTION AND THE ANNUAL GROWTH CYCLE

In a biologically productive region such as the Labrador Sea, characterized by strong seasonal cycles, it is difficult to fully evaluate the system dynamics based on sampling for only a brief period once per year, as has been the operational mode for the Atlantic Zone Off-shelf Monitoring Program. Satellite ocean colour data, collected for the region since 1998, has helped to fill in some of the critical observational gaps to provide a better understanding for the spatial and temporal variability of phytoplankton and primary productivity in the Labrador Sea. Despite the presence of ice along the coasts, as well as clouds and fog that obscure the satellite signal, sufficient data have been

collected in the Labrador Sea area over the past 15 years, along with the field data described above, to provide a fairly synoptic view of the major spatial and temporal features and growth dynamics of phytoplankton in the region. Composite imagery for the region, for example, has shown the major season growth events which include a remarkable (and early) spring bloom off the coast of Greenland, followed by a pulse of growth in the western Labrador Basin just off the Labrador coast and extending down to the Newfoundland slope waters, and a very narrow band of growth at the Labrador Shelf edge in fall extending from Hudson Strait to southern Labrador (Figure 11).

Another perspective of the seasonal growth dynamics can be seen in contour plots of SST and ocean colour along the L3 line (Li and Harrison 2014: Figures 2-6, 9-12). Most evident in the temperature fields is the influence for much of the year of cold arctic-origin coastal currents along the western (Labrador) and eastern (Greenland) boundaries of the L3 Line and the considerably warmer central Labrador Basin. Prominent features of the chlorophyll fields are the early and intense bloom on the Greenland coast, extending well into the Labrador Basin, the slightly later bloom on the Labrador coast and the early summer bloom off the Labrador Shelf. Note that the general sampling schedule for the Atlantic Zone Off-shelf Monitoring Program in May and June, effectively captures the major phytoplankton growth event in the region.

The geographically synoptic and regular (bi-weekly) record of satellite data are well-suited for evaluating the regional and inter-annual dynamics of the spring bloom in the Labrador Sea area. Based on both SeaWiFS and MODIS data, the bloom was consistently earliest, average ~May 16th (DOY 136) on the Greenland Shelf compared with ~May 30th (DOY 150-51) on the Labrador Shelf and ~June 17th (DOY 164-171) in the central Labrador Basin (Table 8). The amplitude of the bloom was also highest on the Greenland Shelf, averaging 4.12-5.87 mg m^{-3} compared with 1.95-3.16 mg m^{-3} on the Labrador Shelf and 1.52-1.65 mg m^{-3} in the central Labrador Basin (for the MODIS time series, see Li and Harrison 2014: Figure 13). In contrast, the duration of the bloom was greatest in the Labrador Basin, average ~155 d, compared with 54-61 d on the Labrador and Greenland Shelves.

Synoptic satellite data are also amenable to a more ecological relevant partitioning of the Labrador Sea area than the relatively crude "boxes" that we have used up to now (see Figure 1). For example, we have begun to explore new spatial indicators of blooms areal extent (based on chlorophyll thresholds) to complement our temporal indicators of timing, amplitude and duration. As a start, we have chosen >1 and >2 mg CHL m^{-3} as alternate thresholds for the start and end of the bloom and mapped the area encompassing these values relative to the area of the Labrador Sea (Figure 12). Using SeaWiFS data (1999-2004), the >1 mg m^{-3} "patch" covers almost 30% or 3.0*10^{5} km^{2} of the Labrador Sea area (1.0 *10^{6} km^{2}) at its maximum in spring and the >2 mg m^{-3} "patch" covers almost 15% or 1.4*10^{5} km^{2} (Figures 13 and 14). The summer and fall

blooms (see Figure 11) are also apparent in the >1 mg m^{-3} trace while only the spring and fall are seen in the >2 mg m^{-3} trace. Bloom areal extent using these criteria also varies considerably from year-to year, ranging from 25-55% (Figure 15). This analysis can be simply extended to compute the inventory of chlorophyll (kg) in the bloom as the product of the area and concentration. In a similar way, the contribution of the bloom to the annual regional primary production can be easily determined. This latter quantity is of considerable importance to ecosystem energy flow, structure and function.

3.3 MODELED VERSUS MEASURED "SIMULATED" IN-SITU (SIS) PRODUCTIVITY

The amassed information on chlorophyll and photosynthetic parameters for the NW Atlantic over the past two decades, archived in the DFO BIOCHEM database[2], has underpinned the development of an operational production model driven by satellite input data (SST, chlorophyll, irradiance) with the potential for generating production estimates on km – ocean basin / weekly – annual spatio-temporal scales (Platt et al. 2008). Preliminary computations have been completed for the Labrador Sea area using SeaWiFS (chlorophyll and irradiance inputs) and NOAA Pathfinder (SST inputs) data for the years 1998-2004. These estimates aligned well with field measurements ("simulated" *in situ* experiments, SIS) made during the same time period (Table 9). Modeled productivity estimates ranged from 664-1,050 mgC m^{-2} d^{-1} on the Labrador Shelf, 734-1,062 mgC m^{-2} d^{-1} in the Labrador Basin and 683-1,125 mgC m^{-2} d^{-1} on the Greenland Shelf. SIS productivity estimates were more variable, considerably fewer in number, and generally higher than the model estimates, ranging from 403-2,178 mgC m^{-2} d^{-1} on the Labrador Shelf, 693-1,426 mgC m^{-2} d^{-1} in the Labrador Basin and 457-3,071 mgC m^{-2} d^{-1} on the Greenland Shelf. NO_3-based "new" production (Eppley and Peterson 1979) estimates from the ^{15}N tracer experiments (see Methods) ranged from 181-1,499 mgC m^{-2} d^{-1} (38-91% of total) on the Labrador Shelf, 202-751 mgC m^{-2} d^{-1} (29-75% of total) in the Labrador Basin and 171-2,457 mgC m^{-2} d^{-1} (18-80% of total) on the Greenland Shelf. Annual production estimates from the model output ranged from 130-154 gC m^{-2} y^{-1} on the Labrador Shelf, 139-154 gC m^{-2} y^{-1} in the Labrador Basin and 138-155 gC m^{-2} y^{-1} on the Greenland Shelf, all strikingly similar despite differences seen in the sub-regional chlorophyll cycles. The contribution of the spring bloom to the total annual production can also be approximated (see previous section). Using model-fitted bloom parameters (Table 8), where the start and end (duration) of the bloom is defined as 3.59σ (or ~20% of the bloom amplitude), the bloom accounted for ~59% of the annual production on the Labrador Shelf, ~98% in the Labrador Basin and ~77% on

[2] http://www.meds-sdmm.dfo-mpo.gc.ca/biochem/biochem-eng.htm

the Greenland Shelf. Using the simpler and more restrictive threshold of >1 mg CHL m^{-3}, the bloom accounted for only ~35%, ~34% and ~39% of the annual production in those sub-regions, respectively.

4. DISCUSSION

4.1 SPATIAL-TEMPORAL VARIABILITY

Spatial-temporal variability in environmental and photophysiological properties observed during this study are consistent with results from our earlier studies in temperate to sub-arctic waters (Harrison and Platt 1986). Depth dependence of P-I parameters (Table 2) reinforced the notion of increased photosynthetic efficiency and photo-adaptation to low light levels in the sub-surface chlorophyll maximum layer and below. Geographical differences in environmental and photosynthetic properties were also observed (Table 3, Figures 3-6), largely related to the regional circulation and water mass characteristics (Head et al. 2003, Yashayaev 2007). Cold boundary current and elevated phytoplankton biomass (chlorophyll concentrations) on the Labrador and Greenland shelves and west-to-east gradients in nutrient concentrations and ratios (decreasing) and P-I parameters (increasing) were prominent features. Time of year of sampling contributed most to the observed variability in environmental and photosynthetic properties (Tables 4-7). Maximum particulates and phytoplankton biomass were seen in spring and minimum in winter, varying by an order of magnitude. P-I parameters, with the exception of anomalously low values in fall, were surprisingly similar year-round, varying by much less than a factor of 2.

Inter-annual variability for all properties was high and thus long term trends were generally hard to detect using an averaging scheme that integrates across the entire transect through LSS, CLB, and GSS (Figures 7-10). However, in a more comprehensive station-by-station analysis of the spring/summer AR7W data subset, we (Li and Harrison 2014) draw attention to the following features. First, nutrients (nitrate, phosphate, silicate, excess phosphate) and physical conditions (temperature, salinity, stratification) have a high degree of spatial similarity in their pattern of inter-annual change. Long-term change in these variables is mostly weak everywhere on the transect, but in the few places where change is strong, it is mostly negative (but see also Harrison and Li 2008, Yeats et al. 2010, Rey 2012). Second, the bulk portion of the phytoplankton biomass (as measured by chlorophyll *a*, chlorophyll *c*, fucoxanthin, diadinoxanthin) appear to be strongly increasing on the shelves and slopes (LSS, GSS), but either decreasing or not changing much in CLB.

We now have evidence that the vertical chlorophyll structure (i.e. thickness of the subsurface maximum, σ) may also have increased over time (Figure 9), as did the P-I parameters, including the temperature used for experimental incubations (Figure 10). Indeed, a number of studies have highlighted the role temperature plays in the regulation of photophysiology (Harrison and Platt 1986, Stuart et al. 2000, Bouman et al. 2003, 2005). Temperature and salinity in the 150 - 2000m layer (~mesopelagic zone) of the central Labrador Sea have unequivocally increased since 1994, although the trend is at times punctuated by sharp reversals due to deep winter convection (Yashayaev 2007; Yashayaev et al. 2014a,b). However, in the seasonally active surface layer (~epipelagic zone), multiyear trends in temperature, salinity, and density are more difficult to discern (Li and Harrison 2014) because of at least three factors contributing to short and long term variability: heat exchange with the atmosphere, heat and salt gain from Atlantic source waters, and freshwater input from ice, melt water, continental runoff, and precipitation.

There have been numerous studies of bio-optical properties of waters of the North Atlantic, including the Labrador Sea, describing phytoplankton community composition and size structure, and attempting to relate these properties to environment, photophysiology and productivity (e.g. Stuart et al. 2000, Bouman et al. 2003, 2005, Cota et al. 2003, Lutz et al, 2003, Vidussi et al. 2004, Claustre et a. 2005, Uitz et al, 2006, 2008, Devred et al. 2011). However conclusions have been mixed: correlations between community structure and photosynthetic parameters have, indeed, been observed but have generally been weak. Higher maximum photosynthetic rates (Pmax) have been associated with the larger microphytoplankton (e.g. diatoms) whereas higher photosynthetic efficiencies (α) have been associated more with the nano- and picoplytoplankton components of the communities. Our long-term analysis of pigment composition of Labrador Sea phytoplankton suggest that the larger microphytoplankton increase, on average, from ~60-80% of the community on the Labrador Shelf to almost 100% on the Greenland Shelf whereas the picophytoplankton decrease west to east from ~10-30% on the Labrador Shelf to <10 % on the Greenland Shelf (Li and Harrison 2014). The abundance of nanophytoplankton increases from west to east, but drops off slightly on the Greenland Shelf. Patterns in the distribution of P-I parameters, particularly the decrease in Pmax and Ik on the Greenland Shelf (Figure 6) are most similar to the distribution of nanophytoplankton, and both evidently related to the strong temperature gradient approaching the Shelf. Similarly, the slight increase in Pmax, α and Ik over time (Figure 10) was also seen in the time-series analysis of the composition and size structure of the phytoplankton communities, particularly in the components contributing most to bulk phytoplankton biomass, and especially on the shelves and slopes, LSS and GSS (Li and Harrison 2014).

One of the most conspicuous features of the phytoplankton growth cycle in the Labrador Sea is the early and intense spring bloom in the shelf/slope waters, particularly off the Greenland coast (Figure 11; see also Head et al. 2003, Wu et al. 2008, Frajka-Williams and Rhines 2010, Harrison et al. 2013; Li and Harrison 2014). During the years of the present study (Table 8), the spring bloom off the Greenland coast peaked as early as late April and mid-May on the average. This compared to the average peak of the spring bloom occurring in early June off the Labrador coast and mid to late June in the central Labrador basin. In addition to an earlier bloom off the Greenland coast, its amplitude, at times >10 μg L^{-1} chlorophyll *a* (CHL) and averaging 4-5 μg CHL L^{-1}, was significantly higher than the blooms off the Labrador coast (average peak = 2-3 μg CHL L^{-1}) and the central basin (average peak = 1.5-2 μg CHL L^{-1}). Although more intense on the shelves, the duration of the blooms were shorter (50-60 d) than in the central basin (>150 d). Recent observational and modeling studies in the Labrador Sea have confirmed this phytoplankton growth pattern and explain the early bloom off the coast of Greenland by freshwater-driven (ice melt, enhanced regional precipitation) early onset of stratification, enhanced eddy activity and off-shelf advection (Wu et al. 2008, Frajka-Williams and Rhines 2010). Off the coast of Labrador, ice plays an important role in bloom dynamics (Wu et al. 2007). Others (Frajka-Williams and Rhines 2010) have noted significant inter-annual variability in bloom properties in the Labrador Sea, similar to our observations, with bloom amplitudes varying by a factor of 4 and timing by as much as 3 weeks over a decade of observations.

Physical processes are also likely major drivers for the summer and fall phytoplankton growth in the region. Results from ARGO floats deployed in the Labrador Sea suggest there is a relatively large recirculation zone off the southern coast of Labrador, east of the strong boundary currents where currents are relatively weak (Yashayaev, pers comm). This area coincides approximately with the extent of the summer phytoplankton bloom in the central basin (Figure 11); upper water column stabilization, enhanced by weak currents, likely favours phytoplankton growth there. The distinct fall bloom off the shelf of Labrador is principally driven by shelf-slope mixing processes (Drinkwater and Harding 2001).

4.2 REGIONAL PRODUCTIVITY

The complex hydrographic setting of the Labrador Sea, influenced by strong boundary currents and a recirculating central basin (Yashayaev 2007), account for a correspondingly geographically-structured chemical and biological environment. In most cases, distinctly different nutrient conditions, phytoplankton community composition, photophysiology and phytoplankton growth cycles characterize the shelf and basin sub-regions described above. Primary productivity from our field

measurements fall within the range of values reported for other field studies in sub-polar regions (Goeyens et al. 1991, Cota et al 1996, Rey et al. 2000, Bode et al. 2002, Tremblay et al. 2006, Garneau et al. 2007, Harrison et al. 2013) and estimates based on models and/or remote sensing (Longhurst 2007, Skogen et al. 2007, Wu et al. 2008, Frajka-Williams et al. 2010, Harrison et al. 2013). Our estimates of NO_3-based new production averaged 50-60% of total production, consistent with results from other studies (see references above).

Due to strong seasonal variability and limited field sampling (once/yr), a complete (annual) picture of the productivity of the Labrador Sea has only been possible using productivity models employing remotely-sensed (satellite) and measured chlorophyll fields and P-I parameters (see Methods). This approach generates productivity estimates on the km spatial scale with a weekly to monthly frequency. At the present time, the productivity model we have employed is being refined and not yet fully operational. However, we have made preliminary estimates using our field data and SeaWiFS chlorophyll for the years 1998-2004. Estimates fall within the range of our field measurements although less variable and slightly lower in magnitude (Table 9). In fact, model output suggests that productivity in the Labrador Sea is highly conserved; annual estimates over the 6 years for the three sub-regions ranged from 130-155 gC m^{-2} y^{-1}, despite the considerably larger variance in biomass among years and sub-regions (Table 3, 5, 6; Figures 4, 5). Refinements of these estimates, including the contribution of the spring bloom taking into account spatial extent (Figures 12-15), will be forthcoming. Our initial estimates of the contribution of the spring bloom off the Greenland coast, where it is most prominent (see Figure 12), ranged from 39-77% of the annual production depending on the criteria used for initiation and termination of the bloom.

Longer term temporal trends in some environmental properties (e.g. temperature, SiO_3 deficit) and photophysiology (phytoplankton community structure and P-I parameters) in the Labrador Sea were not reflected in productivity where measured and modeled total and new production showed no trends, although the latter were a short series (6 y). However, a longer series (20 y) has suggested that the timing of the bloom and peak productivity in the Labrador Sea has been somewhat earlier in recent years (Harrison et al 2013). Other model studies of the high arctic, in the presence of a substantially decreasing ice mass, have not detected any trends in productivity in areas upstream of the Labrador Sea as a consequence (Arrigo et al. 2008, 2011, Pabi, 2008). However, it seems that in recent years with a delay in freeze up and an increased exposure of the sea surface to wind stress, conditions in the high Arctic Ocean may be increasingly favourable for the development of phytoplankton blooms in the fall as well (Ardyna et al. 2014).

This study has attempted to summarize the spatial-temporal variability in photophysiology, productivity and associated environmental properties of the Labrador

Sea derived from 20 years of sea-going measurements and satellite observations. Although largely descriptive, this report should serve as a starting point for more insightful investigation of the productivity of the region and the underlying regulatory mechanisms that will help address pressing issues related to ecosystem structure and function and the impacts of and feedbacks to a changing climate.

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TABLES

Table 1. Labrador Sea missions, 1991-2011. P-I = photosynthesis-irradiance experiments, SIS = simulated in-situ productivity experiments.

Mission	Year	Sampling Dates	Year Day (avg)	P-I Stns (#)	SIS Stns (#)
1991-007	1991	22 May - 31 May	147	10	
1994-008	1994	27 May - 09 Jun	153	31	
1995-016	1995	09 Jul - 16 Jul	194	7	
1996-006	1996	18 May - 30 May	143	13	
1996-026	1996	25 Oct - 18 Nov	310	18	
1997-009	1997	14 May - 09 Jun	148	26	
1998-023	1998	27 Jun - 07 Jul	184	9	
1999-022	1999	6 Jul - 11 Jul	187	14	14
2000-009	2000	24 May - 07 Jun	150	26	7
2001-012	2001	04 Jun - 13 Jun	159	11	11
2002-032	2002	02 Jul - 15 Jul	190	14	18
2002-075	2002	01 Dec - 09 Dec	339	10	
2003-038	2003	23 Jul - 01 Aug	208	12	9
2004-016	2004	21 May - 29 May	145	7	7
2005-016	2005	29 May - 02 Jun	151	6	
2006-019	2006	26 May - 04 Jun	150	11	
2007-011	2007	11 May - 21 May	136	11	
2008-009	2008	23 May - 30 May	147	5	
2009-015	2009	18 May - 26 May	142	10	
2010-014	2010	17 May - 24 May	141	5	
2011-009	2011	10 May - 21 May	136	10	
TOTAL:				266	66

Table 2. Summary statistics of nutrients, particulates and P-I parameters (see Methods) in the Labrador Sea by depth of sampling. NO_3 = nitrate, PO_4 = phosphate, SiO_3 = silicate, CHL = chlorophyll a, POC = particulate organic carbon, PON = particulate organic nitrogen, Pmax = maximum photosynthetic rate (mgC $mgCHL^{-1}$ h^{-1}), α = photosynthetic efficiency [mgC $mgCHL^{-1}$ h^{-1} (W m^{-2})], Ik = photo-adaptation parameter, Pmax/α (W m^{-2}), incubation temperature (°C).

Depth	Variable	# Obs	Min	Max	Average	Stdev
Shallow (0-10 m)						
	Nutrients	240				
	NO_3		0.00	16.86	6.10	4.50
	PO_4		0.02	2.18	0.55	0.27
	SiO_3		0.00	12.56	4.00	2.88
	Particulates	259				
	CHL		0.14	21.90	3.00	3.75
	POC		30	1284	288	225
	PON		4	322	47	43
	P-I Params	266				
	α		0.01	0.24	0.063	0.045
	Pmax		0.08	14.59	2.16	1.37
	Ik		5	156	40	21
	Incub Temp		-1.5	11.1	3.8	2.5
Mid-depth (15-30 m)						
	Nutrients	178				
	NO_3		0.00	14.20	6.75	3.99
	PO_4		0.13	1.07	0.61	0.20
	SiO_3		0.13	10.68	4.25	2.83
	Particulates	187				
	CHL		0.14	24	2.73	3.43
	POC		27	1304	242	185
	PON		4	188	39	31
	P-I Params	187				
	α		0.01	0.70	0.082	0.073
	Pmax		0.11	12.53	2.31	1.40
	Ik		7	103	34	17
	Incub Temp		-1.6	10.8	3.4	2.4
Deep (40-60 m)						
	Nutrients	57				
	NO_3		0.15	14.37	8.53	3.78
	PO_4		0.07	1.17	0.7	0.21
	SiO_3		0.23	11.58	5.35	2.83
	Particulates	62				
	CHL		0.15	10.28	1.8	2.03
	POC		41	676	188	121
	PON		5	91	29	21
	P-I Params	62				
	α		0.01	0.19	0.083	0.042
	Pmax		0.29	5.66	2.02	1.05
	Ik		8	75	27	12
	Incub Temp		-1.5	7.9	2.7	2.4

Table 3: Summary statistics of nutrients, particulates, chlorophyll profile parameters (see Methods) and P-I parameters in the Labrador Sea by sub-region. Bo = background chlorophyll (mg m^{-3}), Zmax = depth of sub-surface chlorophyll maximum (m), σ = index of the width or thickness of subsurface chlorophyll maximum (m), h = chlorophyll integral under the Gaussian curve (mg m^{-2}). See Table 2 for definition of other variables.

Region	Variable	# Obs	Min	Max	Average	Stdev
Labrador Shelf/slope						
	Nutrients	87				
	NO_3		0.00	15.20	4.86	4.15
	PO_4		0.20	1.17	0.62	0.22
	SiO_3		0.00	11.58	4.91	3.14
	Particulates	90				
	CHL		0.15	20.13	3.03	4.10
	POC		38	620	217	157
	PON		5	322	42	56
	Chl Profiles	63				
	Bo		0.00	1.40	0.29	0.36
	Zmax		0	57	17	13
	σ		6	71	18	13
	h		2	1278	202	280
	P-I Params	90				
	α		0.01	0.14	0.06	0.03
	Pmax		0.56	3.95	1.94	0.81
	Ik		15	118	39	18
	Incub Temp		-1.6	11.1	1.9	2.7
Central Labrador Basin						
	Nutrients	203				
	NO_3		0.00	15.06	8.21	3.71
	PO_4		0.07	1.70	0.62	0.22
	SiO_3		0.04	8.40	4.59	2.62
	Particulates	225				
	CHL		0.14	12.17	2.07	2.07
	POC		27	1011	229	165
	PON		4	151	36	27
	Chl Profiles	169				
	Bo		0.00	4.88	0.30	0.67
	Zmax		0	73	19	12
	σ		7	53	25	10
	h		1	829	154	149
	P-I Params	215				
	α		0.01	0.42	0.08	0.05
	Pmax		0.40	6.26	2.41	1.04
	Ik		8	156	37	21
	Incub Temp		0.5	9.9	4.4	1.6
Greenland Shelf/slope						
	Nutrients	41				
	NO_3		0.00	15.20	4.86	4.15
	PO_4		0.02	1.12	0.44	0.22
	SiO_3		0.00	8.03	3.27	2.53
	Particulates	41				
	CHL		0.31	24.00	4.24	5.76
	POC		79	1304	341	268
	PON		9	146	51	36
	Chl Profiles	38				
	Bo		0.00	7.17	1.02	1.78
	Zmax		1	60	20	15
	σ		7	53	21	15
	h		3	1776	251	424
	P-I Params	39				
	α		0.02	0.70	0.11	0.11
	Pmax		0.83	8.46	2.84	1.66
	Ik		12	88	34	20
	Incub Temp		-0.1	6.3	2.5	2

Table 4: Summary statistics of nutrients in the Labrador Sea by month of sampling. See Table 2 for definition of variables.

Month	Variable	# Obs	Min	Max	Average	Stdev
May		237				
	NO_3		0.00	15.20	7.59	4.49
	PO_4		0.02	1.12	0.61	0.23
	SiO_3		0.00	10.06	5.42	2.51
June		101				
	NO_3		0.00	14.37	5.59	3.87
	PO_4		0.10	1.48	0.58	0.25
	SiO_3		0.14	11.58	4.32	3.10
July		92				
	NO_3		0.02	16.86	4.20	3.00
	PO_4		0.10	2.18	0.51	0.26
	SiO_3		0.00	12.56	1.25	1.66
October		30				
	NO_3		0.43	13.42	9.22	3.45
	PO_4		0.22	1.70	0.69	0.30
	SiO_3		0.43	6.81	4.21	1.49
December		15				
	NO_3		2.24	13.45	8.40	3.71
	PO_4		0.51	0.90	0.69	0.12
	SiO_3		1.74	5.87	3.88	1.24

Table 5: Summary statistics of particulates in the Labrador Sea by month of sampling. See Table 2 for definition of variables.

Month	Variable	# Obs	Min	Max	Average	Stdev
May		252				
	CHL		0.18	24.00	3.34	4.00
	POC		41	1304	282	205
	PON		4	322	48	42
June		110				
	CHL		0.15	19.01	3.24	3.61
	POC		62	1284	337	239
	PON		6	180	51	36
July		106				
	CHL		0.18	8.72	1.68	1.62
	POC		53	556	195	124
	PON		8	103	31	23
October		30				
	CHL		0.22	7.56	1.43	2.10
	POC		42	344	134	93
	PON		5	49	18	15
December		17				
	CHL		0.14	0.38	0.20	0.07
	POC		27	69	40	13
	PON		4	8	5	2

Table 6: Summary statistics of chlorophyll profile parameters in the Labrador Sea by month of sampling. See Table 3 for definition of variables.

Month	Variable	# Obs	Min	Max	Average	Stdev
May		198				
	Bo		0.00	7.17	0.57	1.05
	Zmax		0	79	21	16
	σ		2	71	23	12
	h		6	1776	227	286
June		89				
	Bo		0.00	1.64	0.28	0.43
	Zmax		0	35	17	9
	σ		5	48	18	10
	h		13	997	140	189
July		89				
	Bo		0.00	0.99	0.18	0.22
	Zmax		0	60	21	13
	σ		4	43	21	11
	h		3	860	111	147
October		19				
	Bo		0.00	0.41	0.18	0.18
	Zmax		0	73	22	21
	s		4	200	55	63
	h		0	441	127	129
December		6				
	Bo		0.12	0.34	0.20	0.11
	Zmax		3	57	29	24
	σ		6	42	20	17
	h		0	4	2	2

Table 7: Summary statistics of P-I parameters in the Labrador Sea by month of sampling. See Table 2 for definition of variables.

Month	Variable	# Obs	Min	Max	Average	Stdev
May		252				
	α		0.01	0.70	0.08	0.07
	Pmax		0.43	14.59	2.37	1.57
	Ik		5	156	36	19
	Incub Temp		-1.6	6.6	2.6	1.9
June		110				
	α		0.02	0.17	0.06	0.03
	Pmax		0.57	5.90	1.90	0.78
	Ik		8	118	35	19
	Incub Temp		-1.5	7.5	3.2	2.2
July		106				
	α		0.02	0.22	0.07	0.04
	Pmax		0.40	5.20	2.59	0.94
	Ik		7	104	43	19
	Incub Temp		-1.4	11.1	5.8	2.7
October		30				
	α		0.01	0.03	0.01	0.01
	Pmax		0.08	0.55	0.25	0.10
	Ik		13	47	25	9
	Incub Temp		0.5	6.5	4.7	1.6
December		17				
	α		0.06	0.16	0.11	0.03
	Pmax		1.61	3.07	2.52	0.46
	Ik		18	29	23	3
	Incub Temp		0.4	5.0	3.3	1.7

Table 8: Bloom parameters (see Methods) from satellite data in the Labrador Sea by sub-region, 1998-2011. Timing = day of year (DOY) of maximum chlorophyll concentration, Amplitude = maximum chlorophyll concentration (mg m^{-3}) at the peak, σ = index of width of the bloom where 3.59 σ approximates bloom duration (days).

Region	Year	SeaWiFS			MODIS		
		Timing	Amplitude	σ	Timing	Amplitude	σ
Labrador Shelf/slope							
	1998	141	2.61	25			
	1999	152	3.34	19			
	2000	170	1.28	38			
	2001	162	2.86	18			
	2002	175	2.13	27			
	2003	159	2.52	14	154	2.73	14
	2004	148	3.02	21	159	1.30	10
	2005	133	2.83	12	149	1.36	26
	2006	124	3.88	15	135	1.36	31
	2007	165	1.98	16	175	1.16	12
	2008	135	7.78	7	143	1.68	24
	2009				164	2.55	13
	2010	138	3.58	15	135	3.55	14
	2011				153	2.17	14
	2012				145	1.67	14
	Avg	***150***	***3.16***	***19***	***151***	***1.95***	***17***
Central Labrador Basin							
	1998	166	1.68	33			
	1999	177	0.87	66			
	2000	178	1.69	19			
	2001	178	1.41	70			
	2002	175	2.57	15			
	2003	169	1.52	44	146	2.69	12
	2004	184	1.34	43	182	1.08	73
	2005	181	1.50	57	186	1.24	59
	2006	150	2.39	11	145	1.68	12
	2007	176	1.30	73	162	1.28	71
	2008	146	4.08	12	148	2.83	14
	2009				176	0.84	47
	2010	172	1.52	77	182	1.25	61
	2011				165	1.02	96
	2012				152	2.10	19
	Avg	***171***	***1.82***	***43***	***164***	***1.65***	***43***
Greenland Shelf/slope							
	1998	142	3.98	15			
	1999	154	5.93	8			
	2000	132	1.67	28			
	2001	147	9.50	8			
	2002	118	2.52	6			
	2003	130	12.96	17	134	10.67	18
	2004	133	2.62	7	129	4.62	11
	2005	141	2.49	7	119	2.48	7
	2006	134	12.44	7	132	6.32	11
	2007	143	6.15	23	137	3.93	19
	2008	147	8.94	7	139	1.28	8
	2009				153	1.97	19
	2010	182	1.24	72	128	1.94	29
	2011				134	5.80	13
	2012				142	3.21	17
	Avg	***142***	***5.87***	***17***	***136***	***4.12***	***15***

Table 9: Comparison of measured (SIS) and modeled (P-I) total primary productivity, Ptot, and NO3-based "new" productivity, Pnew, (mgC m^{-2} d^{-1}) in the Labrador Sea by sub-region, 1999-2004.

Region	Year	Method	# Obs	Min Ptot	Max Ptot	Avg Ptot	Avg Pnew
Labrador Shelf/slope							
	1999	SIS	4	572	1545	936	421
	2000		1	403	403	403	234
	2001		2	806	1075	941	543
	2002		3	1404	2616	2178	1499
	2003		2	272	887	580	181
	2004		1	279	279	279	254
	1999	P-I	13025	353	1510	781	
	2000		12279	348	2362	773	
	2001		9508	301	2076	834	
	2002		10681	335	2179	758	
	2003		19925	439	1858	1050	
	2004		9411	245	2161	664	
Central Labrador Basin							
	1999	SIS	5	492	824	693	202
	2000		6	262	3460	1426	689
	2001		6	771	1230	1013	508
	2002		11	380	3010	1277	645
	2003		7	728	1451	1085	382
	2004		4	561	1340	989	751
	1999	P-I	65681	415	1852	884	
	2000		57723	325	2016	803	
	2001		18547	346	2181	957	
	2002		76302	379	1887	775	
	2003		77800	418	2196	1062	
	2004		55693	264	2252	734	
Greenland Shelf/slope							
	1999	SIS	2	486	707	597	171
	2000		0				
	2001		1	2475	2475	2475	466
	2002		2	275	638	457	296
	2003		0				
	2004		1	3071	3071	3071	2457
	1999	P-I	1105	333	1694	683	
	2000		721	360	2134	819	
	2001		1233	445	2240	1125	
	2002		1407	378	1837	781	
	2003		1481	348	1329	750	
	2004		1331	359	2074	920	

FIGURES

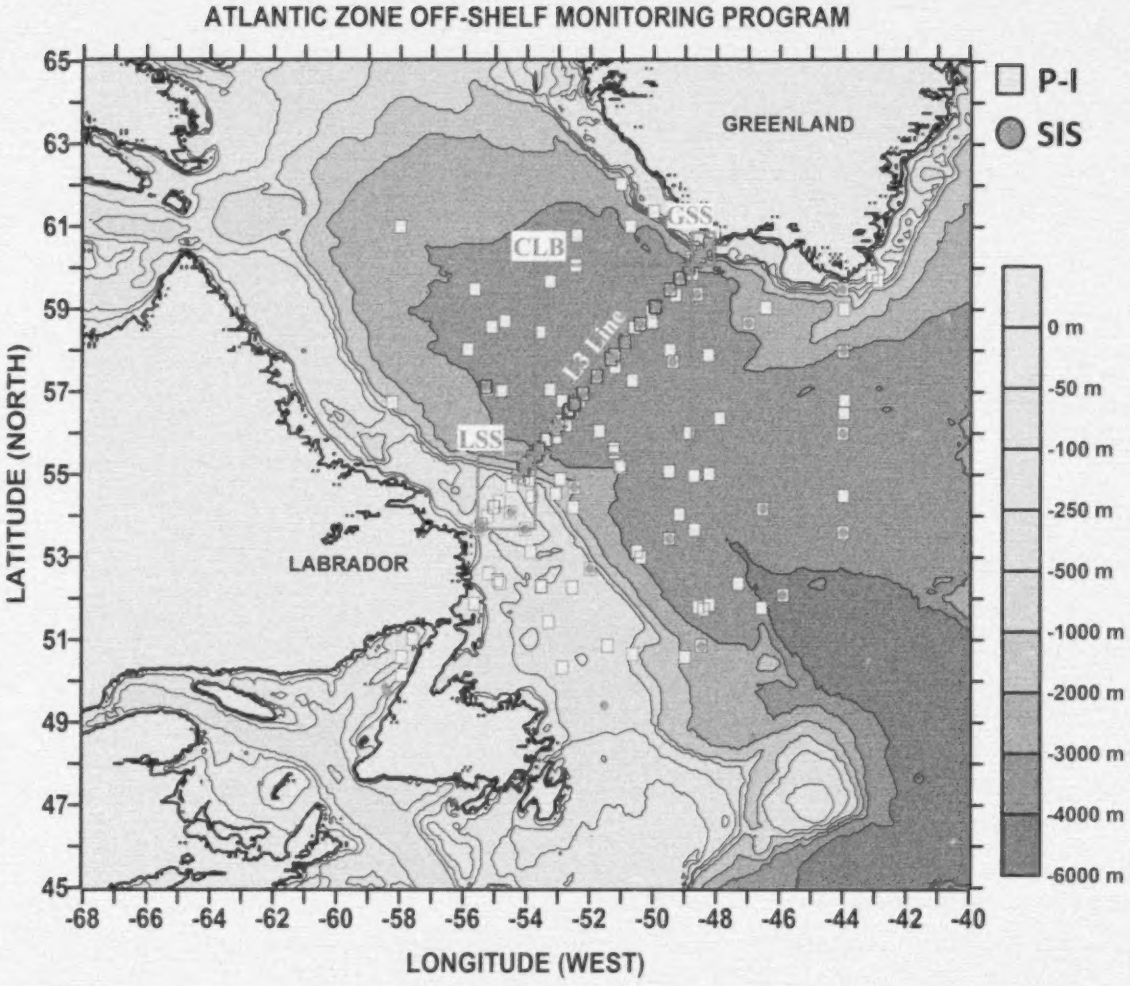

Figure 1: Labrador Sea area primary productivity stations, 1991-2011. Sub-regions: LSS = Labrador Shelf/Slope, CLB = Central Labrador Basin, GSS = Greenland Shelf/Slope. Yellow squares are P-I experimental stations, green circles are "simulated" in situ incubation stations.

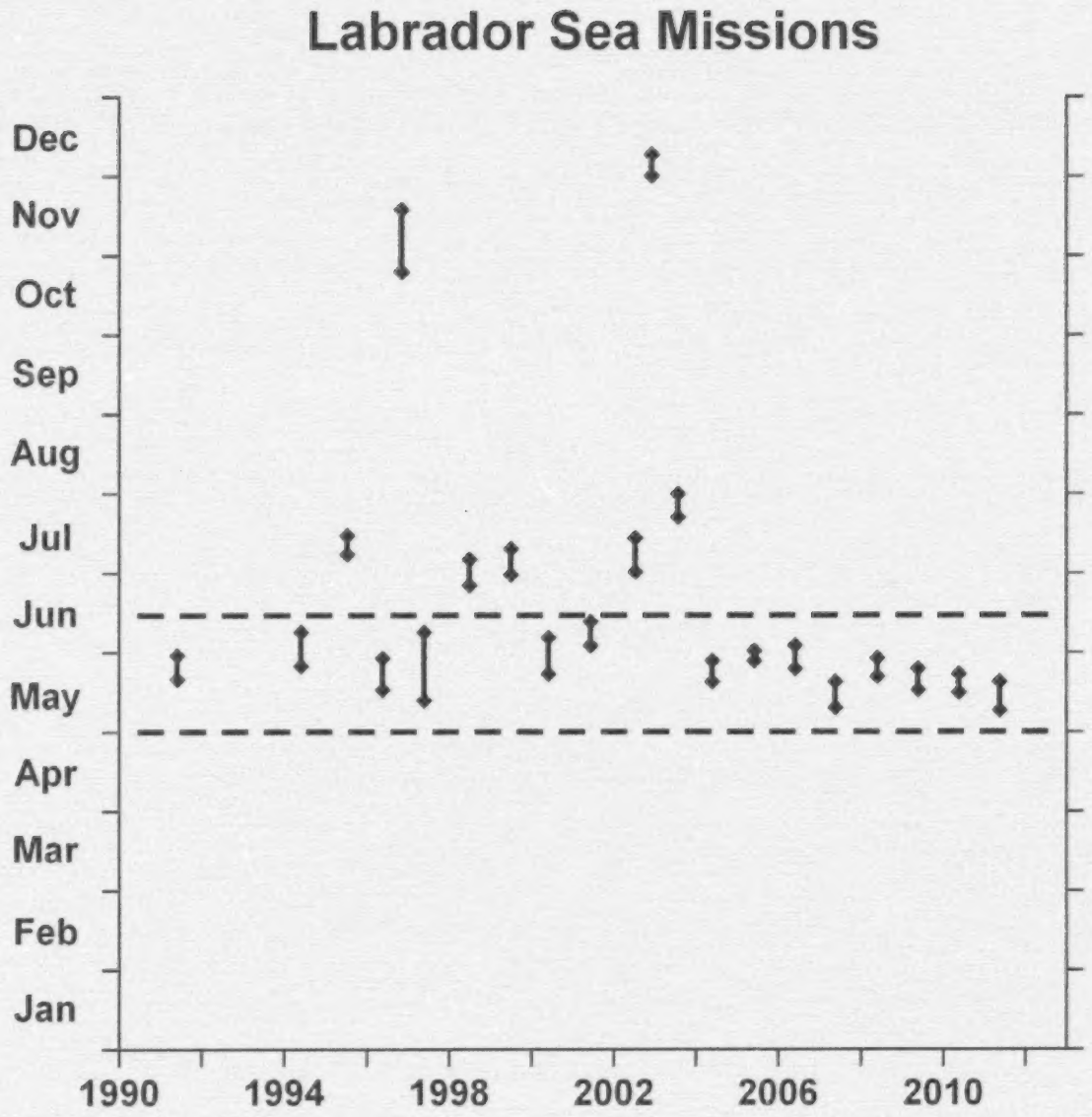

Figure 2: Labrador Sea area mission dates/duration, 1991-2011. Dashed lines indicate missions used in time-series analysis.

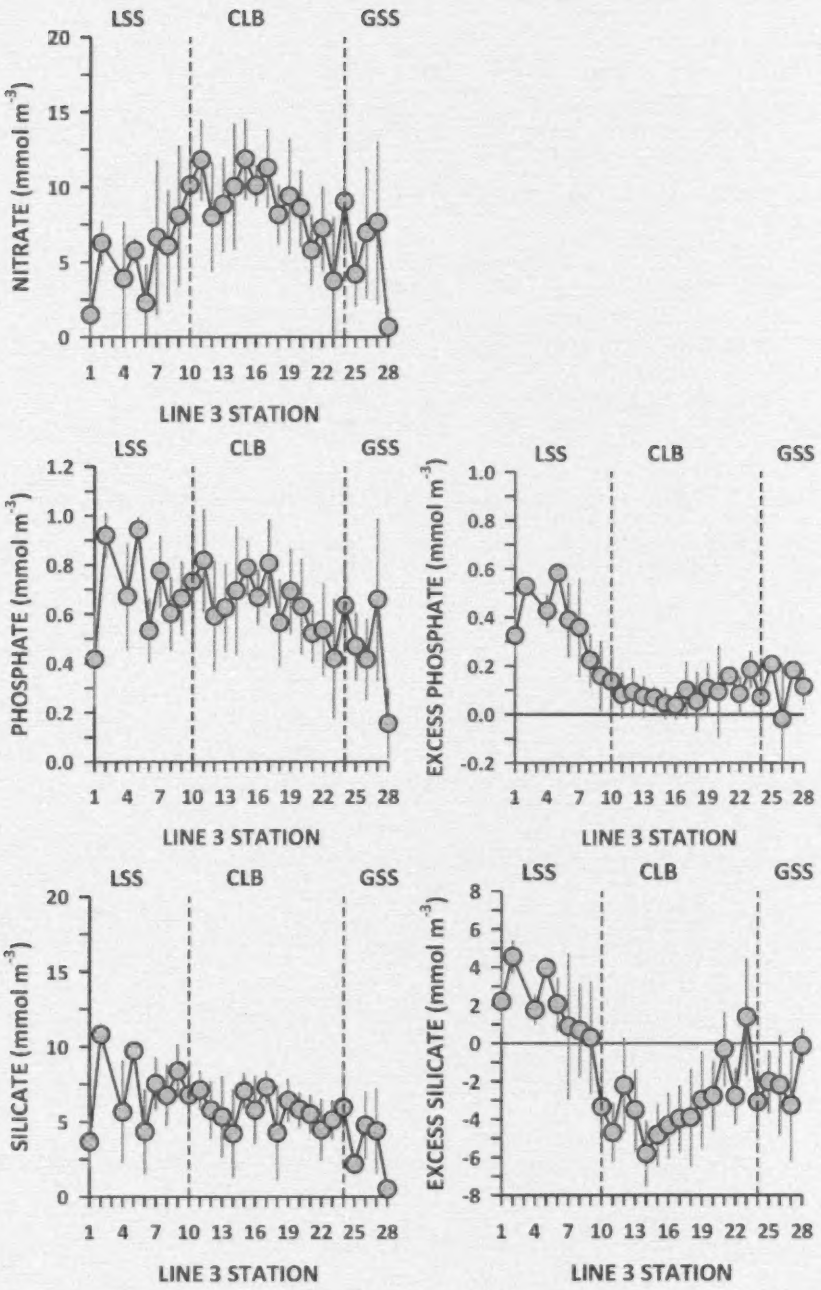

Figure 3: Nutrient concentrations (average ± 1 SD) along the L3 Line, May-June Missions, 1991-2011. Excess phosphate = P-N/16; excess silicate = Si-N. Vertical dashed lines demarcate boundaries of nominal regions LSS, CLB, and GSS.

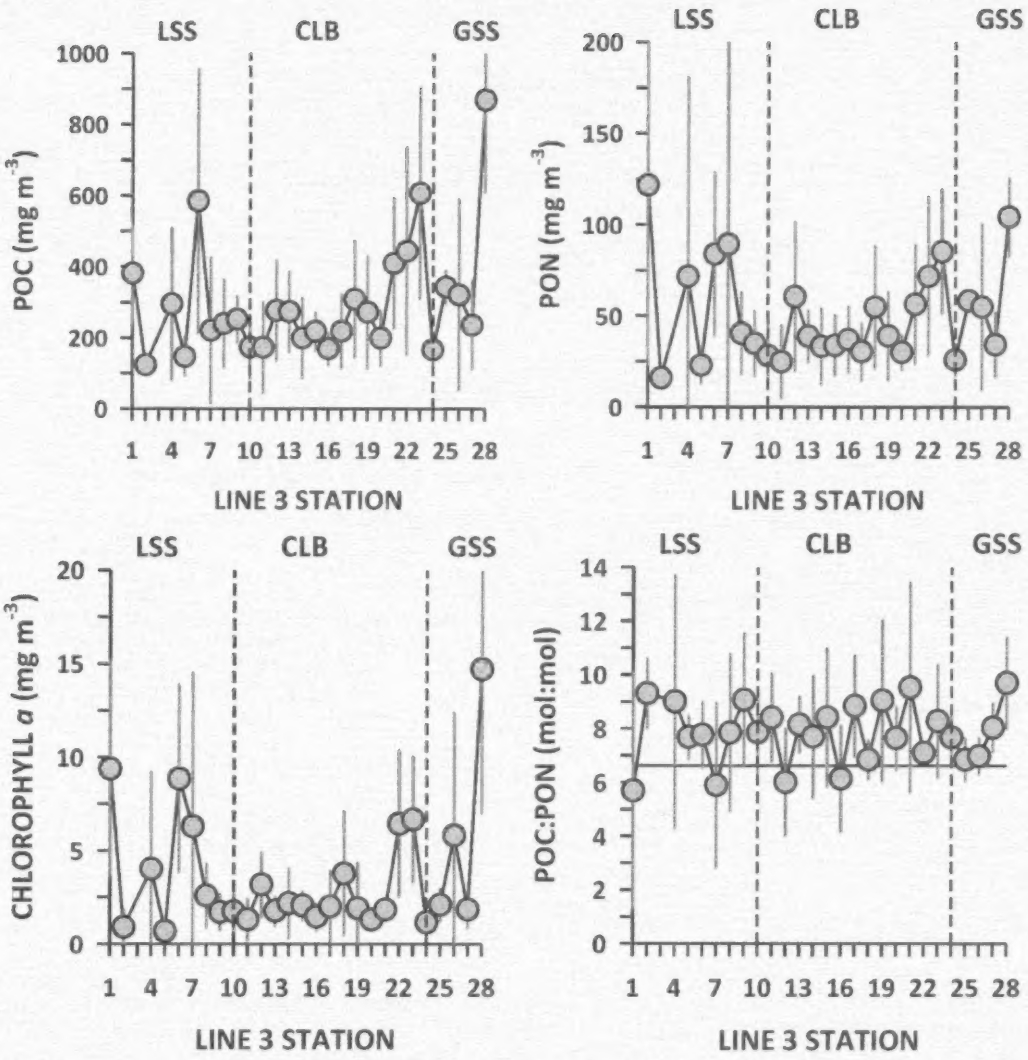

Figure 4: Particulate matter concentrations (average ± 1 SD) along the L3 Line, May-June Missions, 1991-2011. POC = particulate organic carbon, PON = particulate organic nitrogen, POC:PON = molar ratio. Vertical dashed lines demarcate boundaries of nominal regions LSS, CLB, and GSS.

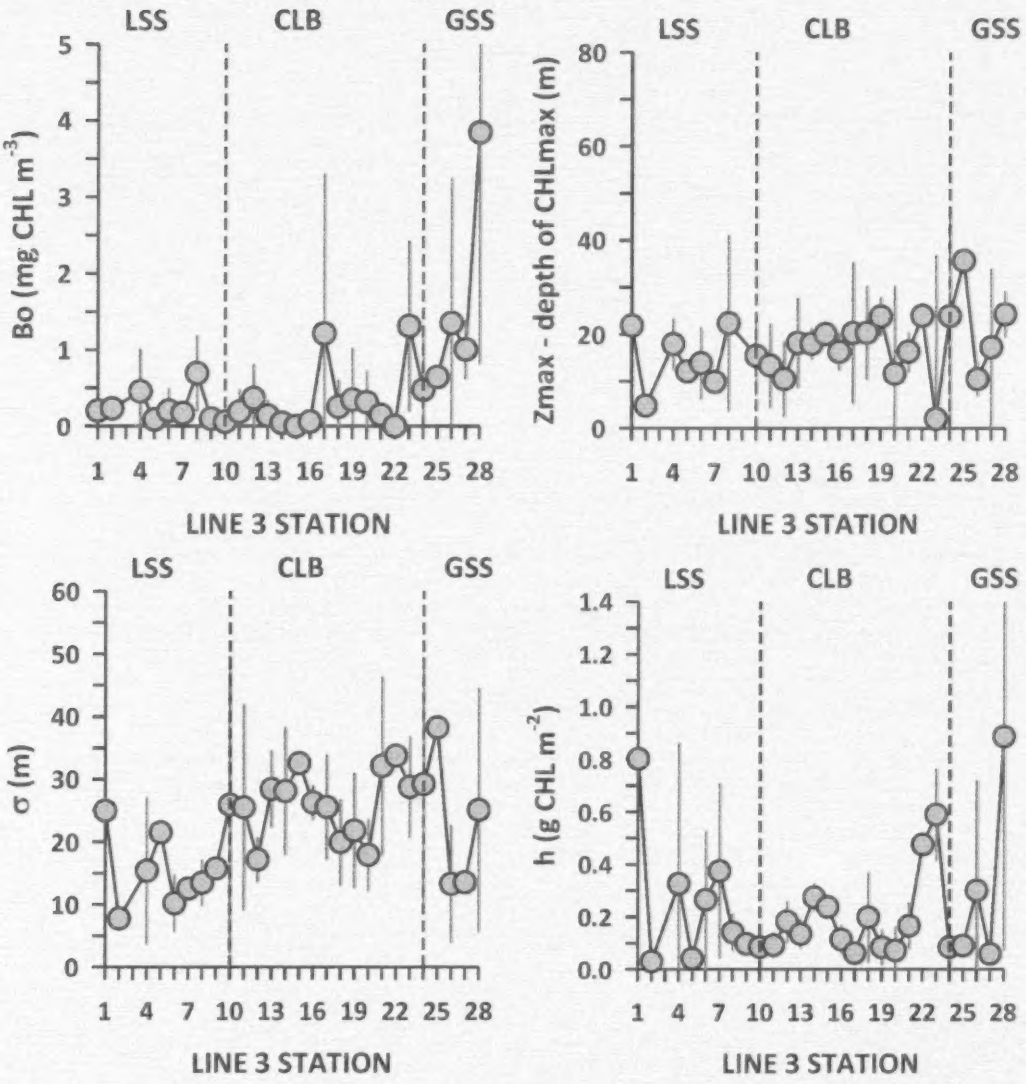

Figure 5: Chlorophyll profile parameters (average ± 1 SD) along the L3 Line, May-June Missions, 1991-2011. Bo = background chlorophyll, Zmax = depth of sub-surface chlorophyll maximum, σ = index of the width or thickness of subsurface chlorophyll maximum, h = chlorophyll integral under the Gaussian curve. Vertical dashed lines demarcate boundaries of nominal regions LSS, CLB, and GSS.

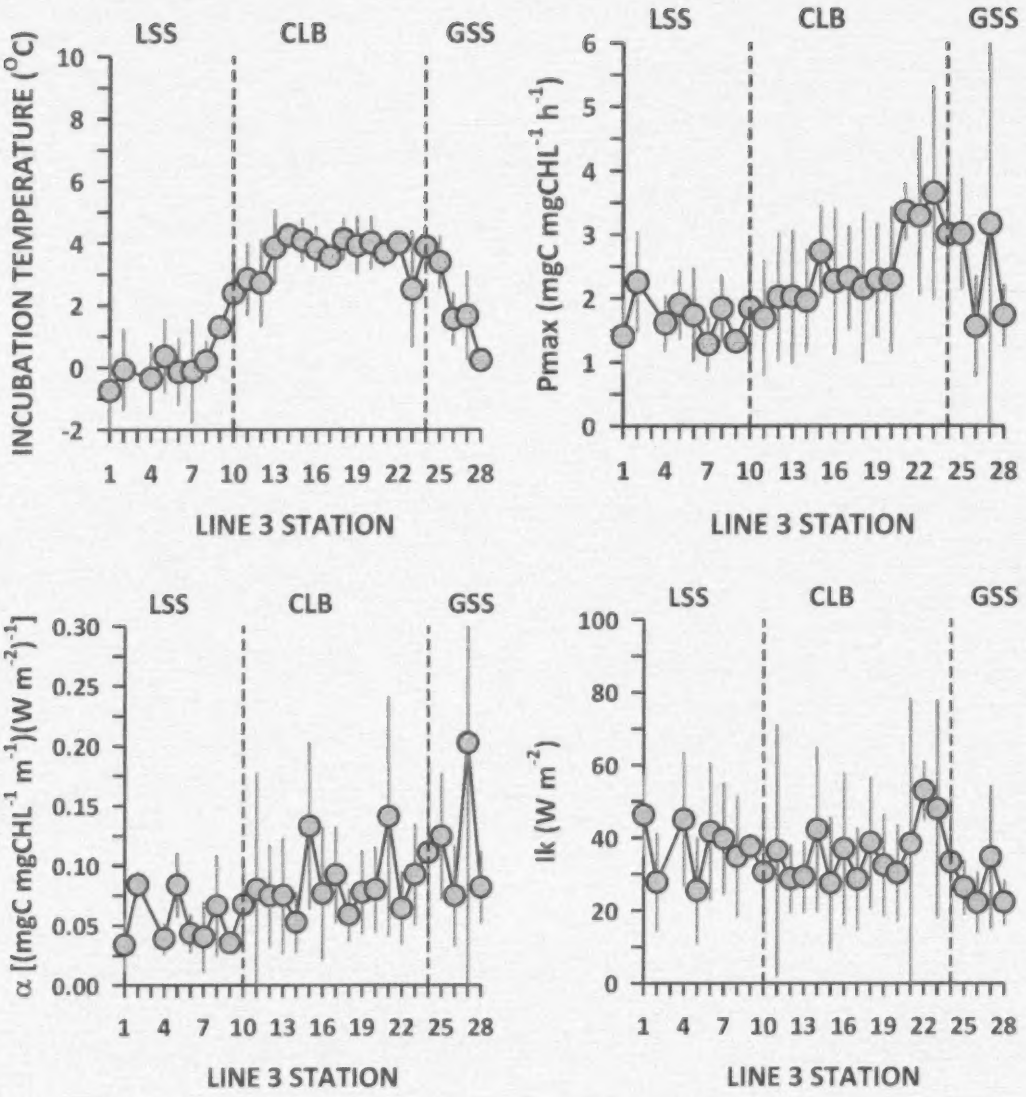

Figure 6: P-I parameters (average ± 1 SD) along the L3 Line, May-June Missions, 1991-2011. Temp = incubation temperature, Pmax = maximum photosynthetic rate, α = photosynthetic efficiency, Ik = photo-adaptation parameter (Pmax/α). Vertical dashed lines demarcate boundaries of nominal regions LSS, CLB, and GSS.

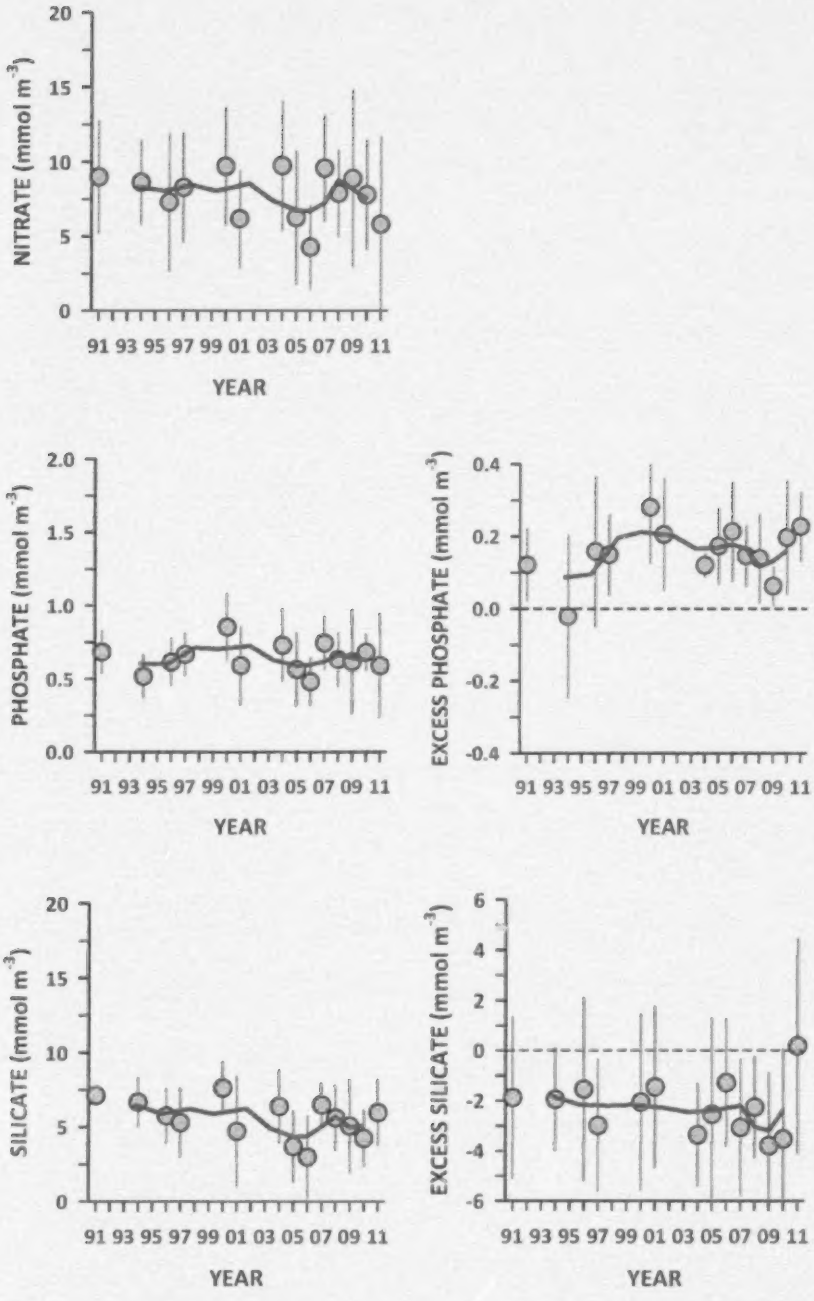

Figure 7: Temporal trends in nutrient concentrations (annual average ± 1 SD) for the L3 Line, May-June Missions. See Figure 3 for definition of variables. Solid line is 3-point running average.

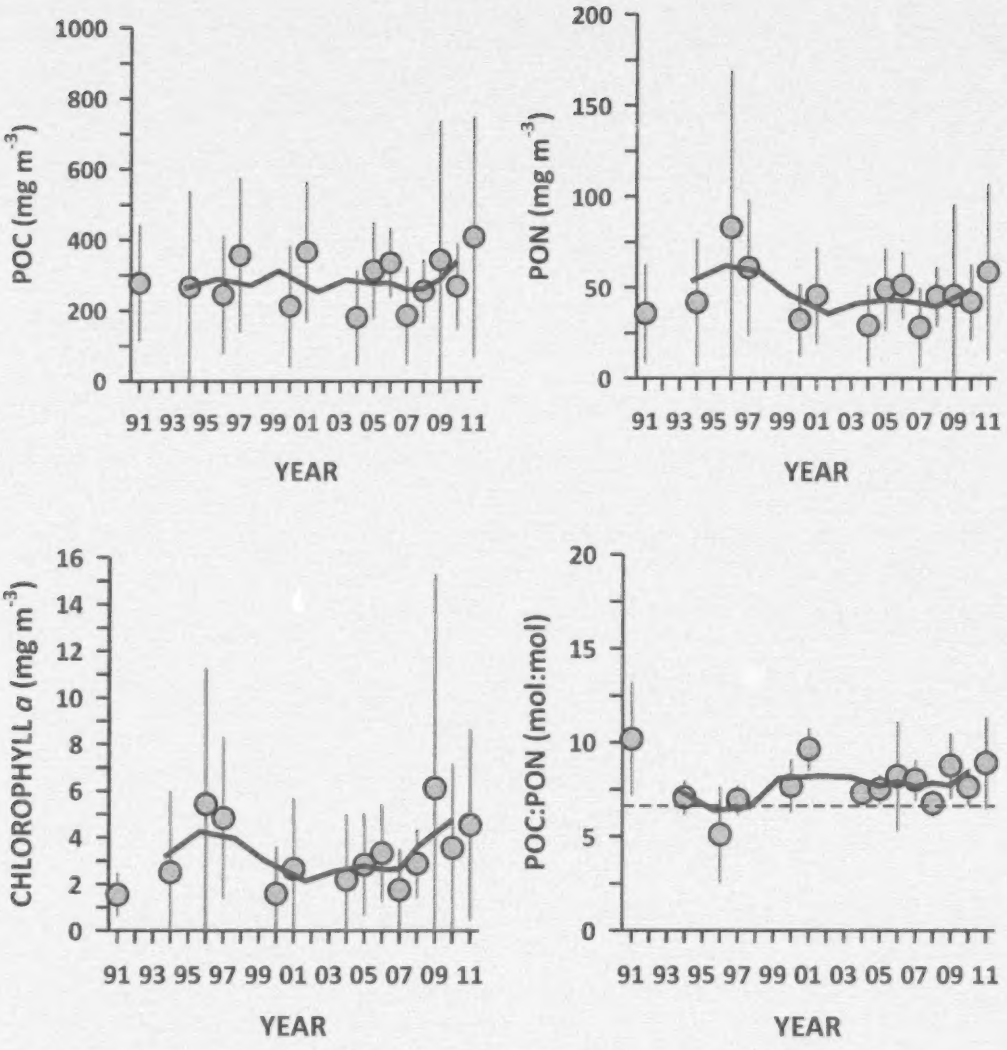

Figure 8: Temporal trends in particulate matter concentrations (annual average ± 1 SD) for the L3 Line, May-June Missions. See Figure 4 for definition of variables. Solid line is 3-point running average.

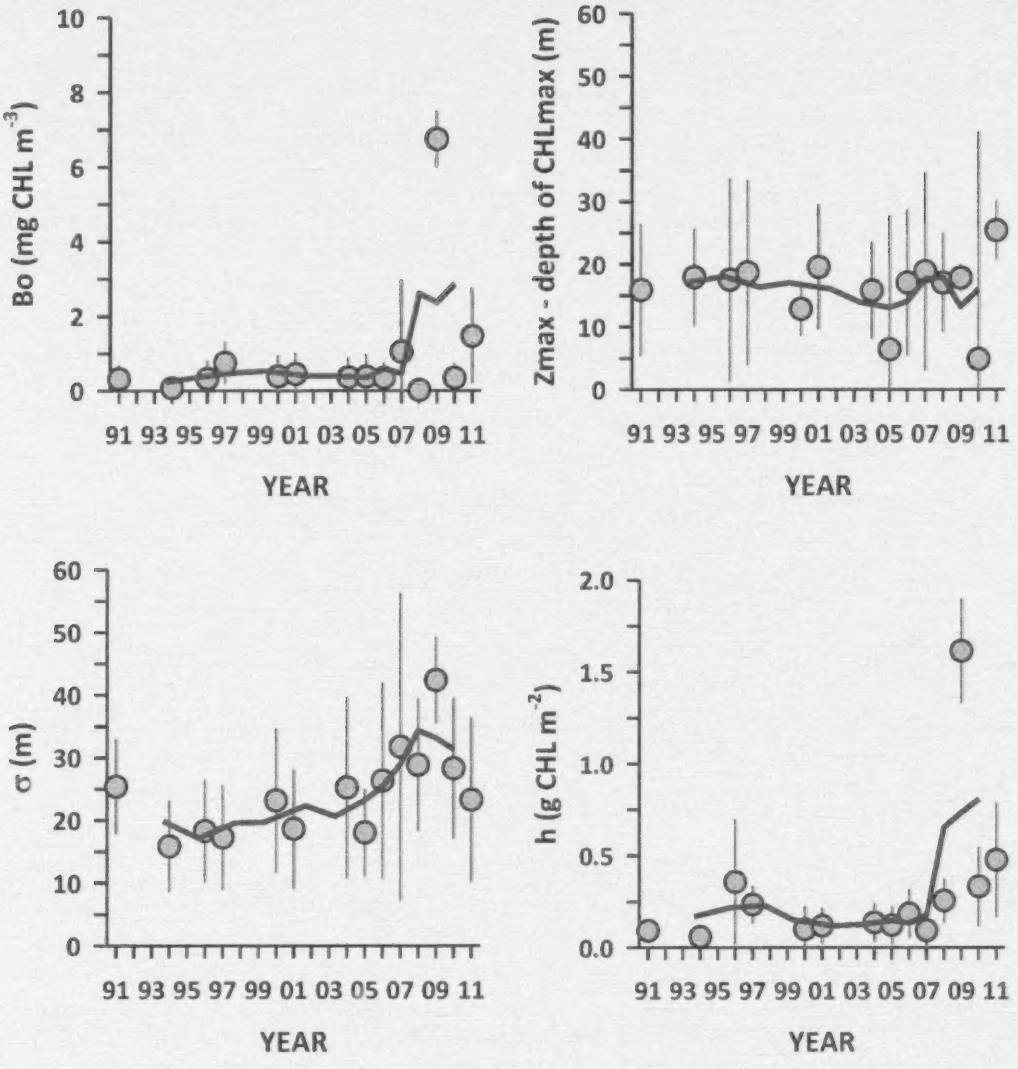

Figure 9: Temporal trends in chlorophyll profile parameter estimates (annual average ± 1 SD) for the L3 Line, May-June Missions. See Figure 5 for definition of variables. Solid line is 3-point running average.

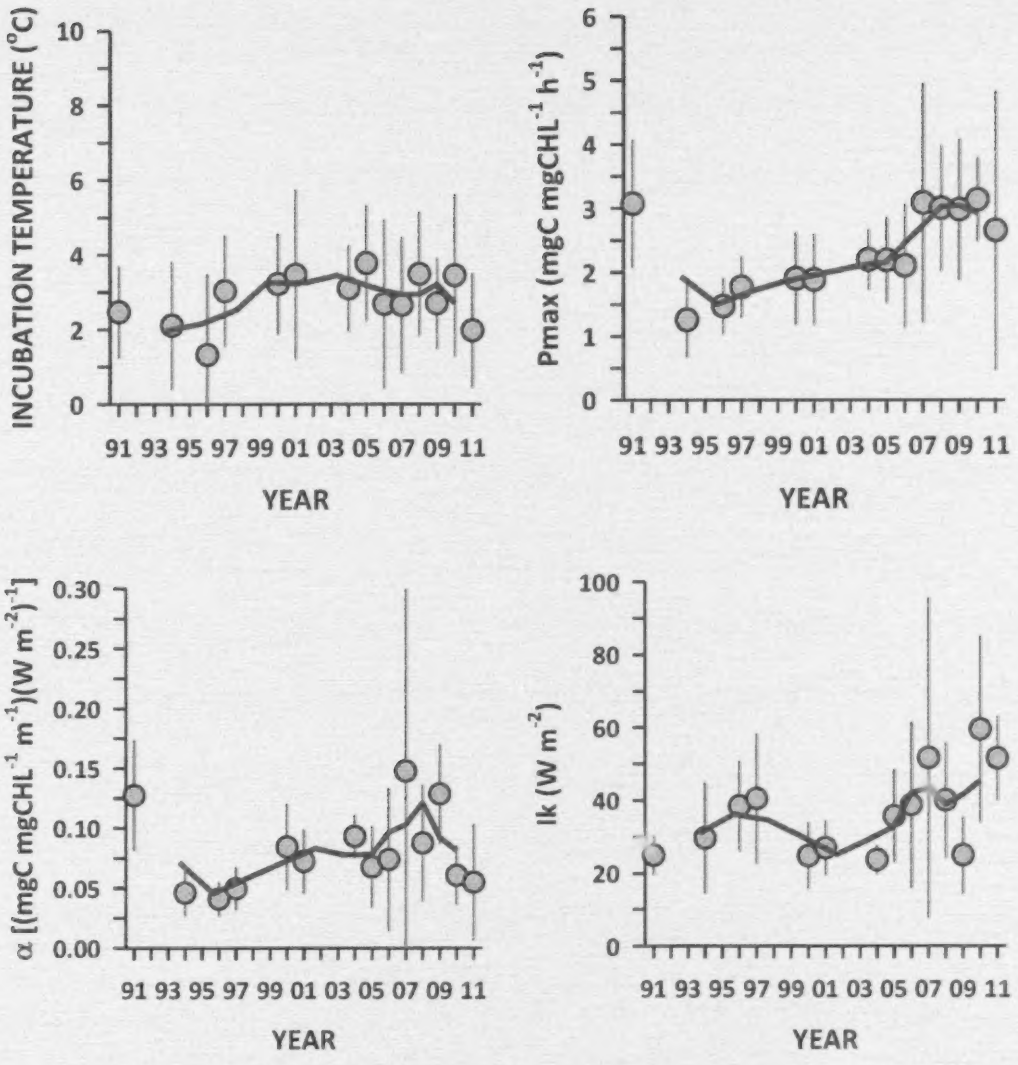

Figure 10: Temporal trends in P-I parameters (annual average ± 1 SD) for the L3 Line, May-June Missions. See Figure 6 for definition of variables. Solid line is 3-point running average.

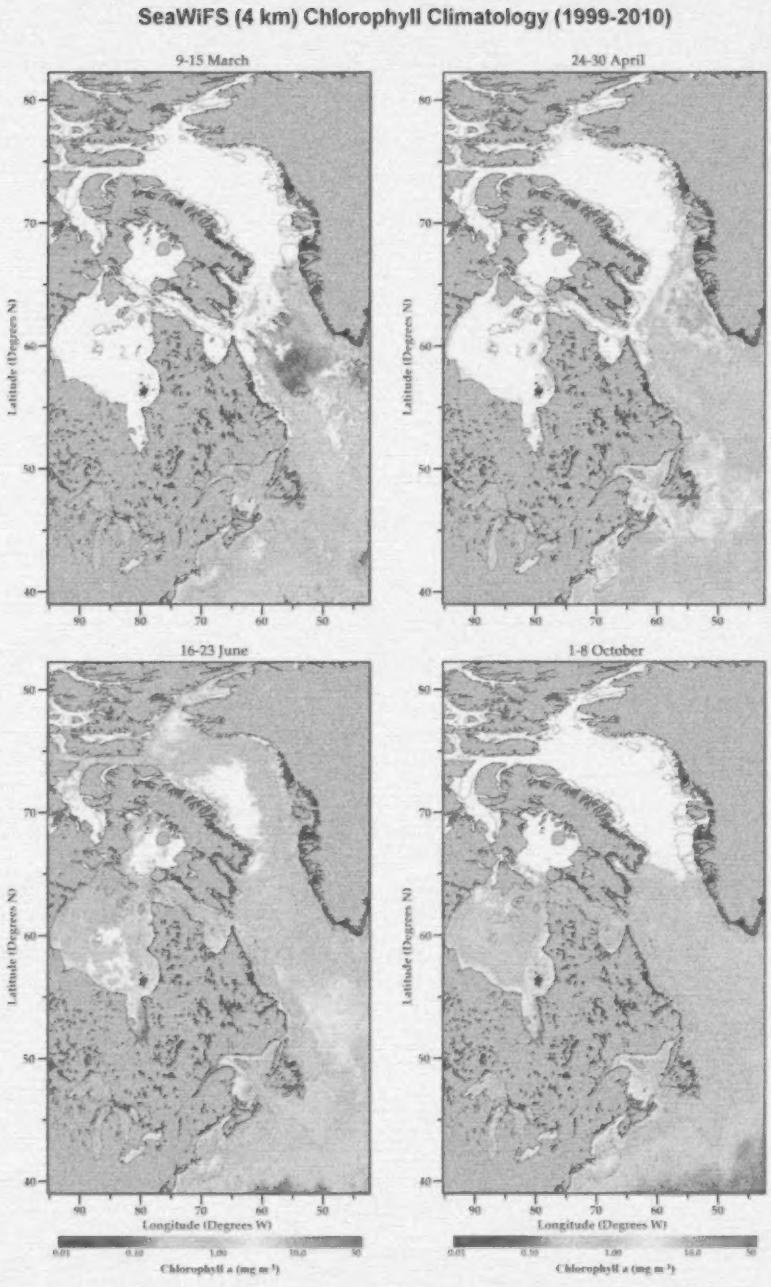

Figure 11: SeaWiFS ocean colour imagery (climatological conditions, 1999-2010) illustrating the major seasonal changes in surface chlorophyll concentrations in the Labrador Sea and adjacent waters.

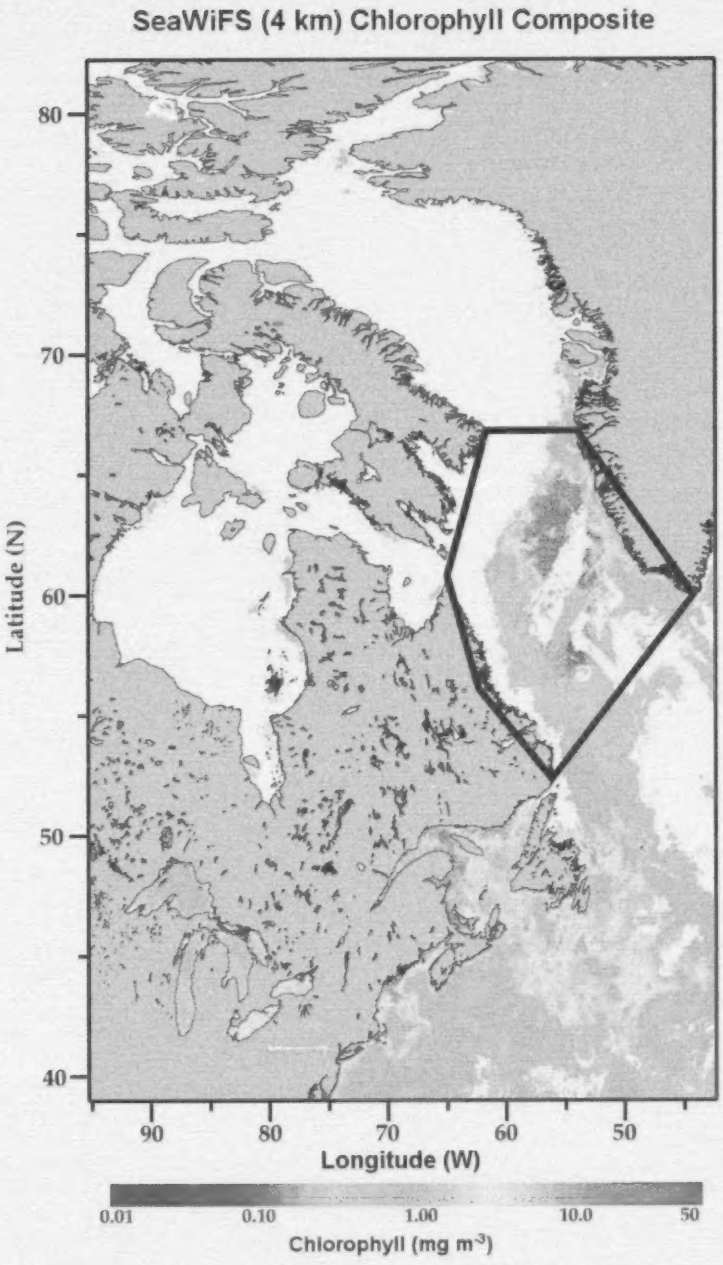

Figure 12: Area (dark lines) defined as Labrador Sea for analysis of areal extent of blooms.

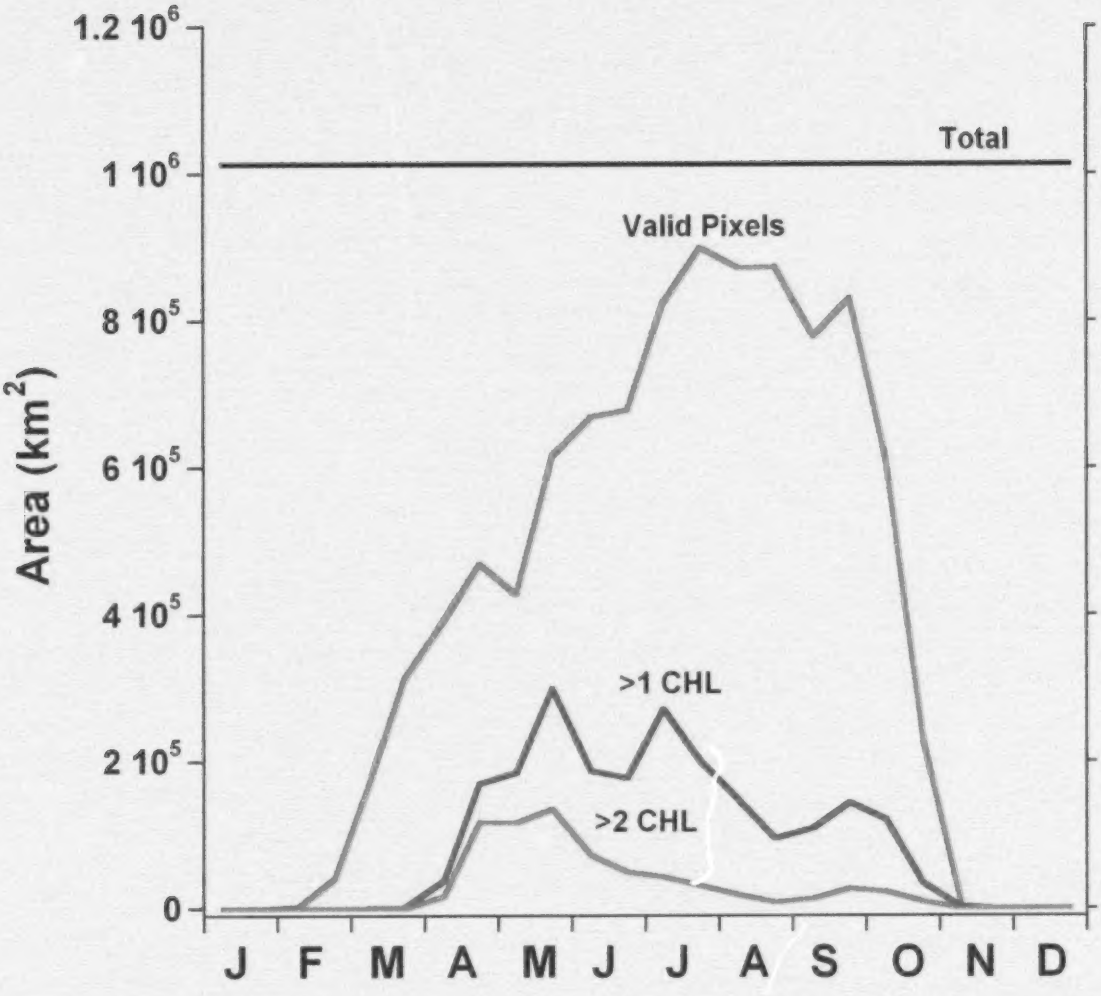

Figure 13: Seasonal changes in area of the Labrador Sea (see Figure 8) covered by valid pixels and where surface chlorophyll concentrations exceed 1 and 2 mg m^{-3}, SeaWiFS climatological conditions (1999-2004).

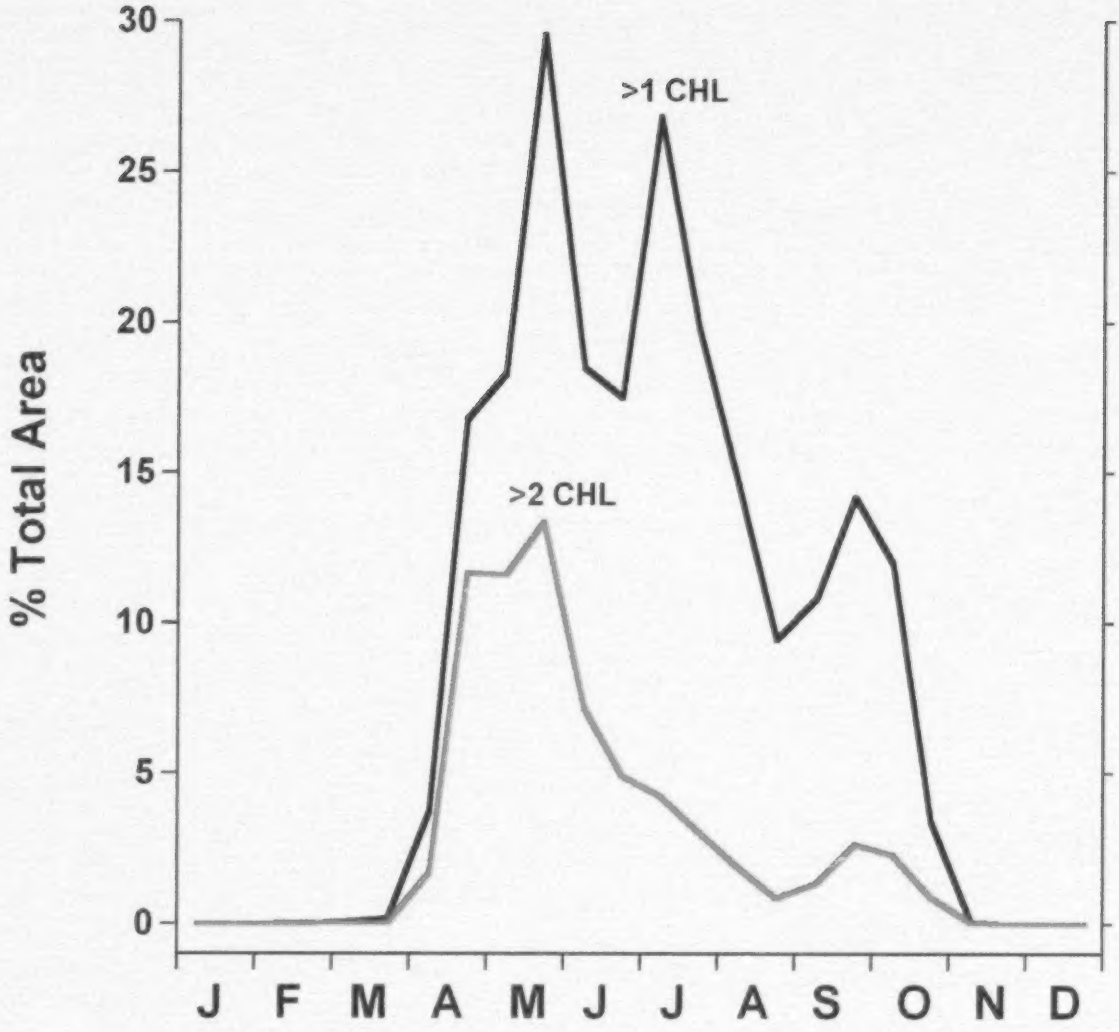

Figure 14: Area (%) of Labrador Sea where surface chlorophyll concentrations exceed 1 and 2 mg m^{-3}, SeaWiFS climatological conditions (1999-2004).

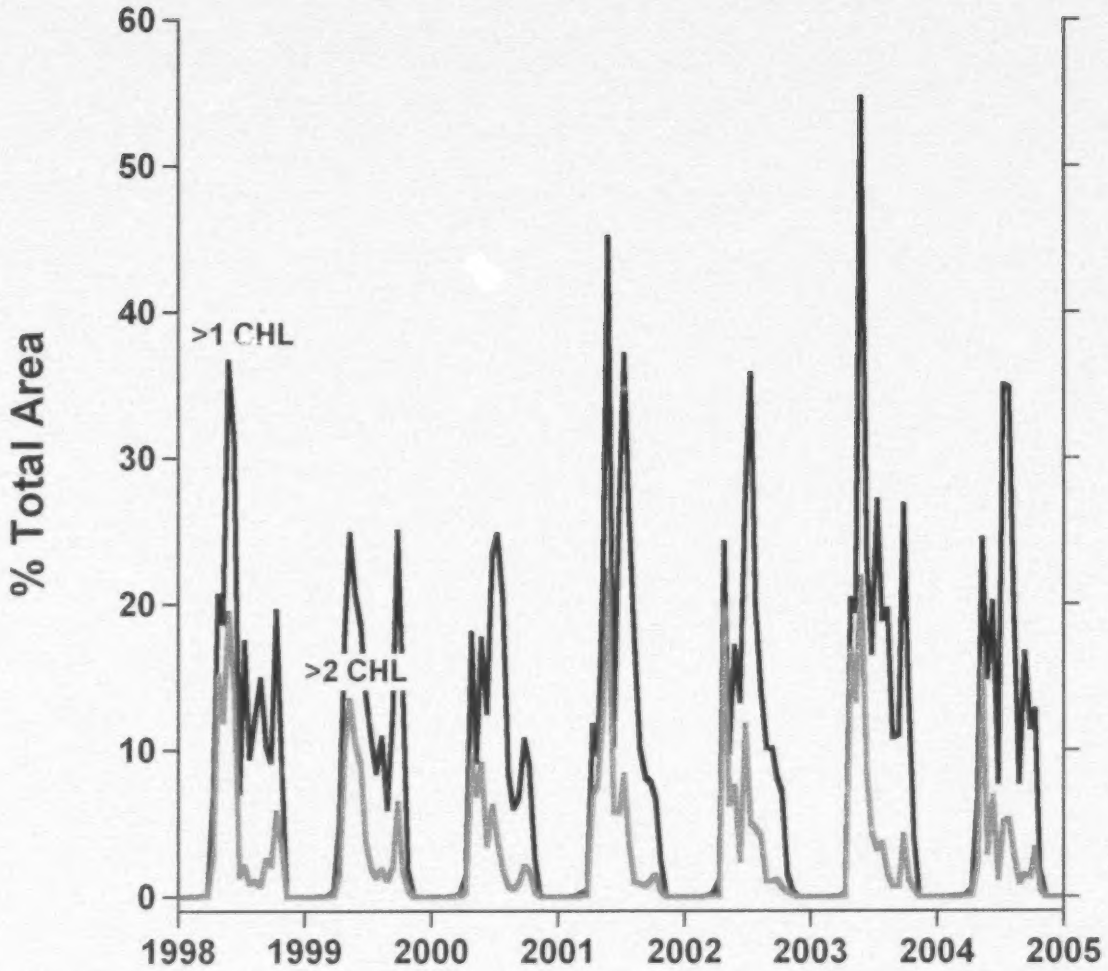

Figure 15: Inter-annual variability in area (%) of Labrador Sea where surface chlorophyll concentrations exceed 1 and 2 mg m^{-3}, SeaWiFS (1999-2004).